

LABORATORY EVIDENCE FOR A SIZE REFUGE IN COMPETITIVE
INTERACTIONS BETWEEN THE HYDROIDS *HYDRACTINIA*
ECHINATA (FLEMMING) AND *PODOCORYNE CARNEA* (SARS)

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ABSTRACT

Size refugia from competition, whereby one organism may grow too large to subsequently be overgrown by a superior spatial competitor, have rarely been documented in marine benthic communities. Size-symmetrical and size-asymmetrical competitive interactions were established between colonies of two hermit crab-associated hydroids, *Hydractinia echinata* and *Podocoryne carnea*, to assess the outcome of competition for space between the two species and its possible size-dependence. In size-symmetrical interspecific contests, *P. carnea* overgrew and killed *H. echinata* in 100% of 74 observed encounters. In size-asymmetrical contests in which *H. echinata* was always the larger colony, *P. carnea* was able to overgrow *H. echinata* in only 55% of 76 contests. *H. echinata* reaches a size refuge from overgrowth by *P. carnea*, but this "safe" size depends on the position occupied by a colony of *H. echinata* on a substrate with respect to physical or biological barriers to growth.

The outcome of intraspecific competition for space between *P. carnea* colonies depends on the relative growth rates of the competitors. In 23 intraspecific contests, the *P. carnea* colony with the highest rate of stolonal growth was always competitively dominant, and also overgrew *H. echinata* most rapidly in the size-symmetrical interspecific encounters. The ability of *P. carnea* to overgrow *H. echinata* in size-asymmetrical contests, however, did not depend on the growth rate of the *P. carnea* colony.

Data on the distribution and abundance of these two species suggest that *P. carnea* recruits to hermit crab shells at a low frequency and is thus a rare member of the hermit crab epifaunal community. The observed differences in interspecific competitive ability may reflect asymmetry in the frequencies with which these species encounter one another. The probability that a colony of *H. echinata* will encounter *P. carnea* is low, hence there will be little selection for interspecific competitive ability in *H. echinata*. The probability that a colony of *P. carnea* will encounter the common *H. echinata* is high; *P. carnea*, therefore, should maintain a mechanism for recognizing and overgrowing this important spatial competitor.

INTRODUCTION

The outcome of interactions between organisms does not remain constant throughout their lives. Encounters between competitors or between predator and prey may be sensitive to the relative sizes of the interacting individuals, and the effect one species has on another consequently may change throughout the ontogeny of those species (Buss, 1980; Werner and Gilliam, 1984). The dependence of many predator-prey interactions on prey size has been well documented in marine benthic communities: prey organisms which by chance escape predation when small may eventually

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grow too large to be consumed by a given predator (Ebling *et al.*, 1964; Paine, 1965, 1976; Dayton, 1971; Birkeland, 1974; Connell, 1975). The ability of some individuals in a population to reach a size refuge from predation may contribute significantly to the maintenance of community diversity and structure (Connell, 1975; Paine, 1976, 1977).

Few studies have examined how the outcome of competitive interactions between species may change as the relative sizes of the competing individuals vary. In several examples with colonial marine invertebrates, the direction of interspecific overgrowth has been shown to depend on the size (thickness) of the competing colonies: species A usually overgrows species B when A is larger, and *vice versa* (Day, 1977; Buss, 1980; Russ, 1982). Size refugia, where an individual of species B eventually reaches a size at which an individual of species A will be unable to overgrow it, may occur when the outcome of competition between two species is size-dependent (Buss, 1980). Size refugia from competition in benthic marine communities have been demonstrated by Buss (1980), in a system involving two bryozoans and a coralline alga in Panama, and by Sebens (1982), in a study of competition between the soft coral, *Alcyonium siderium*, and the compound tunicate, *Aplidium pallidum*, in the Gulf of Maine. In this study, I provide evidence for another example of an inferior spatial competitor, the athecate hydroid *Hydractinia echinata* (Flemming), reaching a size at which it can no longer be overgrown by an otherwise competitive dominant, the closely related hydroid, *Podocoryne carnea* (Sars).

In Long Island Sound and other Atlantic soft-bottom coastal areas, pagurid hermit crabs are extremely abundant, and the gastropod shells they occupy represent a source of hard substratum which supports a unique encrusting fauna (Karlson and Cariolou, 1982; Karlson and Shenk, 1983). *Hydractinia echinata* is one of the most common epifaunal species found on pagurid shells in Long Island Sound; *Podocoryne carnea* is present at much lower frequencies in this community. *H. echinata* and *P. carnea* display aggression towards one another, and in a previous examination of interspecific competitive ability *P. carnea* was shown to overgrow *H. echinata* consistently (Gallien and Govaere, 1974). However, all interactions examined were grossly size-asymmetrical, with a small explant of *H. echinata* placed in contact with a large *P. carnea* colony. This particular combination of colony sizes is only one of many conditions under which colonies may contact one another in natural encounters. The outcome of interspecific competition for space between *H. echinata* and *P. carnea* is examined further here, in both size-symmetrical and *Hydractinia*-biased size-asymmetrical interactions, to determine if *P. carnea* remains the superior spatial competitor across a range of size-specific encounters.

Natural history

Although the zooid morphology differs little between the genera (Goette, 1916; Mills, 1976), *P. carnea* and *H. echinata* display different patterns of basal tissue growth across a substratum. Growth of a colony of *H. echinata* is regulated by two interacting processes, elongation of stolons and expansion of ectodermal mat tissue (Fig. 1a). Stolons branch and anastomose to form intricate networks adherent to the substratum. Mat tissue, which consists of interconnecting gastrovascular canals and interstitial cells sandwiched between ectoderm, grows as a continuous sheet. As the mat tissue expands, it incorporates existing stolons into its structure. The interaction of the growth rates of mat tissue and stolons, combined with factors such as stolon branching frequency, give each colony of *H. echinata* a characteristic growth morphology during ontogeny (McFadden *et al.*, 1984). There is considerable genetic variation in stolon

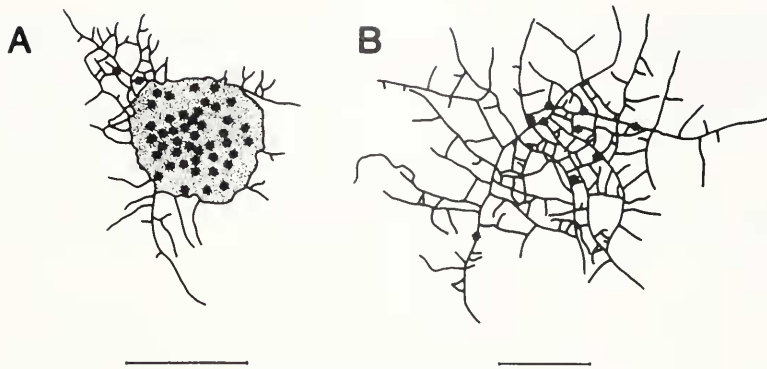


FIGURE 1. Camera lucida tracings of 17-day-old colonies, comparing the growth morphology of *H. echinata* (A) with that of *P. carnea* (B). *H. echinata* produces mat tissue (stippled area) and stolons during colony ontogeny, while *P. carnea* covers the substratum with a stolon network only. Asterisks indicate the positions of feeding polyps. Scale bars = 5 mm.

production: colony morphologies range from "stolonless" colonies which produce little or no stolon tissue as they grow, to "stoloniferous" colonies which form extensive stolon networks throughout colony ontogeny (Schijfsma, 1939; McFadden *et al.*, 1984).

Unlike *H. echinata*, *P. carnea* produces no mat tissue, but covers the substratum with an extensive stolon network (Fig. 1b). This network increases in density by continued proliferation of stolons; adjacent stolons eventually fuse laterally to form a basal crust analogous to the mat of *H. echinata* (Braverman, 1963, 1971, 1974; Braverman and Schrandt, 1966, 1969).

The hyperplastic growth reaction which occurs when genetically unrelated colonies of *H. echinata* contact one another is described in detail elsewhere (Hauenschild, 1954, 1956; Mueller, 1964; Ivker, 1972; Buss *et al.*, 1984). Briefly, nematocyst-bearing hyperplastic stolons arising from both colonies intertwine to form an extensive tangle in the area of contact (Buss *et al.*, 1984), and one colony will eventually overgrow and kill the other (Ivker, 1972). Competitive dominance is strictly transitive (Ivker, 1972), and highly correlated with growth morphology; in size-symmetrical encounters, colonies with high stolon growth rates ("stoloniferous") predictably defeat colonies with slowly growing or no stolons ("stolonless") (Buss and Grosberg, in prep.).

The competitive overgrowth reaction of *P. carnea* is very similar to that of *H. echinata* (Tardent and Buhrer, 1982). Upon contact with a conspecific, stolons raise off the substratum and arch over the neighboring colony, producing a tangle of hyperplastic stolons in the area of contact. Scanning electron micrographs of *P. carnea* hyperplastic stolons show numerous discharged nematocyst threads, indicating that intraspecific overgrowth occurs by the same mechanism in the two genera. Transitivity and morphological correlates of intraspecific competitive ability between colonies of *P. carnea* will be examined briefly here, prior to discussion of interspecific competition.

MATERIALS AND METHODS

The colonies of *H. echinata* and *P. carnea* used in laboratory competition experiments were collected in August 1981 from the shallow subtidal (–3 m) gravel-mud bottom adjacent to No Man's Island, Old Quarry Harbor, Guilford, Connecticut. Individuals of *Pagurus longicarpus* with hydroid-encrusted shells were collected as

encountered using SCUBA and were transported to the laboratory, where small pieces of ectodermal tissue containing 1–3 feeding polyps were excised from each shell. These tissue explants were placed on Plexiglas culture slides and held down by a loop of thread tied around the slide (Ivker, 1972). After 2–3 days, explants attached to the Plexiglas, and the thread was removed. This technique was used for all clonal propagations referred to in this paper. Colonies were maintained at approximately 20°C in recirculating natural seawater, and were fed for 2 h daily with day-old *Artemia* nauplii. Colonies were returned to clean seawater immediately after each feeding. Each slide was brushed weekly with a fine camel's-hair paintbrush to prevent the accumulation of growth-inhibiting detritus.

The use of clonal organisms facilitates an examination of size-specific competitive interactions, because encounters between individuals of the same genotype can easily be replicated over a wide range of size relationships. The competitive ability of an individual which is killed by a competitor when small can nonetheless be examined when the same individual is large by using a clonal replicate, whereas the competitive ability of a non-clonal organism which is killed when small can never be assessed at a larger size. In addition, the degree to which the outcome of a competitive interaction is due to genotypic variation in the competitive ability of the individuals involved can be separated from strictly size-dependent effects by pairing any one individual (genotype) with numerous competitor genotypes.

Intraspecific competition between colonies of P. carnea

Size-symmetrical competitive interactions were initiated between all possible pairwise combinations of four genotypes of *P. carnea* (labeled P1, P2, P3, P4). [The assumption has been made that each field-collected colony represents a unique genotype; potential difficulties with this assumption are discussed in detail in McFadden *et al.* (1984).] Single polyp explants of each of two colonies were established approximately 2 cm apart on Plexiglas slides and allowed to grow into contact with one another. The number of replicates of each pairwise combination varied from 2 to 6, due to difficulties experienced getting explants of some genotypes to attach successfully to slides. The interactions were observed at approximately weekly intervals until tissue of one of the two colonies could no longer be discerned on the slide. In addition, three replicate clones of each of the four genotypes were established as controls to determine colony morphology and growth rate in the absence of competitive interactions. Each control colony was traced at 3-day intervals over a period of 17 days, using a camera lucida attachment to a Wild dissecting microscope at 7.5×. Drawings were digitized using an image analysis system [Measurionics Corp., Linear Measuring Set (LMS)] to determine total length of stolons present at each date. Cumulative growth curves were plotted for each colony, and the slope of the linear regression of the log-transformed curve [$\log(\text{mm stolon}) = m \log(\text{time})$] was used as an index of stolon growth rate. For further discussion of this method for fitting growth curves, see McFadden *et al.* (1984).

Interspecific competition: size-symmetrical contests

Size-symmetrical contests were initiated between 20 genotypes of *H. echinata* (labeled H1–H20) and 4 genotypes of *P. carnea* (P1–P4) in all 80 possible pairwise combinations. Single polyp explants of each species were established 1 cm apart on Plexiglas slides and the interaction of the two colonies was observed at approximately weekly intervals until one colony had completely overgrown the other. Overgrowth

was considered complete when no polyps remained in one of the two colonies. Several colonies died before contact had occurred, including all four replicates of H14; these pairs have been eliminated from the results.

Size-asymmetrical contests

Size-asymmetrical contests were established between clones of the same 20 genotypes of *H. echinata* and 4 genotypes of *P. carnea*. Single polyp explants of *H. echinata* were established on Plexiglas slides and allowed to grow undisturbed for a period of six weeks. At this time they were photographed to record size and general growth morphology, and a single polyp explant of *P. carnea* was then established approximately 1 cm from the periphery (mat edge or outermost stolons) of the *H. echinata* colony. All four clones of genotype H10 appeared unhealthy at the time *P. carnea* was introduced onto the slides and they were therefore eliminated from the experiment.

The interspecific interactions were observed over a period of seven months, at which time the experiment was terminated. Photographs taken of the *H. echinata* colonies at the time of attachment of the *P. carnea* explants were converted to line drawings using a camera lucida on a Wild dissecting microscope at 7.5 \times (McFadden *et al.*, 1984). The area of mat tissue and area covered by stolon network (the polygon determined by connecting the free tips of all stolons) were then digitized using an Apple II graphics tablet to yield estimates of the size and morphology of each *H. echinata* colony just prior to contact with *P. carnea*.

RESULTS

Intraspecific competition between P. carnea colonies

The outcome of intraspecific competition between colonies of *P. carnea* is highly transitive, and can be predicted by stolon growth rate (Table I). P3, the colony with the fastest stolon growth rate, is the competitive dominant; P1, the colony with the slowest growth rate, is consistently overgrown by all other genotypes. Out of 23 contests, the only outcome which deviates from this dominance hierarchy is one of the 3 contests between genotypes P3 and P4. It is possible that the identities of the two colonies on

TABLE I

Mean duration (in days) of intraspecific contests between four genotypes of P. carnea

			Winning genotype			
	Growth rate*		P1	P4	P2	P3
Losing genotype	P1	(1.007)	—	86 (2) S.D. = 42	67 (4) S.D. = 17	70 (6) S.D. = 24
	P4	(1.062)	—	—	122 (2) S.D. = 6	131 (2) S.D. = 19
	P2	(1.319)	—	—	—	179 (6) S.D. = 30
	P3	(1.622)	—	118 (1)	—	—

* Slope of linear regression fit to the log-transformed cumulative growth curve [$\log(\text{mm})/\log(\text{day})$]. Numbers in parentheses indicate number of replicates.

this slide were reversed during the experiment; all other contests involving either P3 or P4 yielded results consistent with predictions based on a transitive hierarchy.

The amount of time required for one *P. carnea* colony to overgrow another depends only on the identity of the losing colony in the contest (Table I; Kruskal-Wallis, within rows, $P < .01$), and not on the identity of the winner (Table I; Kruskal-Wallis, within columns, $P = .42$). For instance, there was no difference in the number of days required for genotypes P2, P3, and P4 to overgrow inferior competitor P1, while the amount of time P3, the competitive dominant, took to overgrow P1, P2, and P4 was highly variable (Table I).

Interspecific competition

H. echinata exhibits little or no hyperplastic growth upon contact with *P. carnea*. Occasionally the growing tips of *H. echinata* stolons swell and rise off the substratum slightly in response to contact with *P. carnea*, but further hyperplastic development rarely occurs. Stolons of *P. carnea* rapidly overgrow *H. echinata* stolons without becoming hyperplastic, but begin hyperplastic growth immediately upon contact with mat tissue. *P. carnea* stolons are unable to grow across mat tissue, and consequently, mounds of hyperplastic stolon up to 5 mm in height accumulate at the periphery of the mat area at every point of contact between *P. carnea* stolons and *H. echinata* mat tissue (Fig. 2). These mounds may extend out over the surrounded mat tissue for as much as 2 cm, but they are not anchored to the underlying mat tissue and are easily broken off. The underlying *H. echinata* polyps are resorbed subsequent to overgrowth



FIGURE 2. A contest between *P. carnea* (P) and *H. echinata* (H). *P. carnea* has produced hyperplastic stolons (S) where it is in contact with *H. echinata* mat tissue.

by *P. carnea* hyperplastic stolons, but if polyps remain alive elsewhere in the colony, the overgrown mat tissue can remain alive. If hyperplastic tissue is removed from the overgrown areas of mat, new polyps may be regenerated on the exposed mat tissue, as is also possible in cases of intraspecific overgrowth in *H. echinata* (Ivker, 1972). Death of the overgrown *H. echinata* colony occurs only when *P. carnea* hyperplastic stolons cover the entire surface of the colony and all the polyps have been resorbed, presumably curtailing nutrient intake and leading to starvation.

Size-symmetrical interspecific contests

In every one of the 74 size-symmetrical contests, *P. carnea* overgrew and killed *H. echinata* (Table II). The mean time for complete overgrowth was 37 days, although several *H. echinata* colonies survived for considerably longer. Genotype H12 withstood overgrowth by P4 for 161 days, eventually with just a single polyp protruding through *P. carnea* hyperplastic stolons. There is a significant association between the duration of a contest and the genotype of the *P. carnea* colony (Kruskal-Wallis, $P < .02$). P3, the fastest growing *P. carnea* genotype, overgrew *H. echinata* in the least time ($\bar{X} = 26$ days), whereas P4, one of the two *P. carnea* genotypes with the slowest growth rates, took the longest time to overgrow *H. echinata* ($\bar{X} = 46$ days) (Table II).

The growth morphology of the *H. echinata* colony does not affect the rate at which it is overgrown by *P. carnea*. Genotypes of *H. echinata* were categorized into three groups based on growth morphology: stolonless, stoloniferous, or intermediate. Morphological category was determined by previous quantitative measures of growth of these genotypes (McFadden *et al.*, 1984), as well as evaluation of the growth of each clone during the experiment. The duration of a contest between *P. carnea* and *H. echinata* did not differ significantly between these three morphological groups (Kruskal-Wallis, $P > .21$).

Size-asymmetrical interspecific contests

Small *P. carnea* successfully overgrew and killed large *H. echinata* in 42 of the 76 size-asymmetrical contests (Table III). In no cases did *H. echinata* overgrow *P. carnea*. The other 34 contests were terminated after approximately 235 days, at which time both species still occupied space on each slide, but the boundary between colonies, delineated by *P. carnea* hyperplastic stolons, had remained static for 2–3 months in all cases. All of these “standoffs” reflected identical situations: *P. carnea* had covered all areas of the slide which were initially vacant or occupied by *H. echinata* stolons, but was unable to overgrow living *H. echinata* mat tissue. Both colonies were substrate-limited by the presence of the other, and further growth could take place only if one colony died or resorbed tissue in the zone of contact.

Unlike the symmetrical contests, there was no significant relationship between the genotype of the *P. carnea* colony and the length of time it took to overgrow *H. echinata* in those asymmetrical contests which ended in the death of the *H. echinata* colony (Kruskal-Wallis, $P > .47$). There was also no significant difference between *H. echinata* morphological types when genotypes were pooled into the categories stolonless, stoloniferous, and intermediate (Kruskal-Wallis, $P > .75$). However, if absolute size of the *H. echinata* colony is examined instead of this qualitative measure of morphology, a significant trend is apparent. Colony size was broken down into two separate measurements, total area covered by mat tissue and total area covered by stolon networks; colony thickness does not change as colony area increases. It has been shown that the growth rates of mat tissue and stolons are largely independent of one another (Mc-

TABLE II

Number of days *H. echinata* colonies survived in size-symmetrical contests

		<i>H. echinata</i> colony																					
		H1	H2	H3	H4	H5	H6	H7	H8	H9	H10	H11	H12	H13	H14	H15	H16	H17	H18	H19	H20	\bar{X}	S.D.
Morphology:		L	I	S	S	S	I	S	I	L	I	I	L	L	L	L	S	I	S	I	S		
<i>P. carnea</i> colony																							
P1		43	32	26	32	27	32	32	32	39	62	87	32	16	—	74	32	32	35	74	29	40	19
P2		13	32	35	29	32	35	62	37	27	25	32	32	32	—	62	20	—	32	70	32	36	14
P3		21	23	35	20	29	16	16	20	32	32	16	35	22	—	28	—	32	32	35	24	26	7
P4		32	32	20	35	32	35	37	27	23	58	35	161	32	—	79	16	51	27	95	51	46	34

L = stolonless, I = intermediate, S = stoloniferous.

TABLE III

Number of days H. echinata colonies survived in size-asymmetrical contests

		<i>H. echinata</i> colony																			
		H1	H2	H3	H4	H5	H6	H7	H8	H9	H10	H11	H12	H13	H14	H15	H16	H17	H18	H19	H20
Morphology:		L	I	S	S	S	I	S	I	L	I	I	L	L	L	L	S	I	S	I	S
<i>P. carnea</i> colony																					
P1		182	120	122	A	A	59	A	66	94	—	A	67	67	107	79	A	192	158	A	A
P2		182	117	122	213	A	25	A	48	55	—	158	51	67	67	A	A	A	A	A	A
P3		159	59	A	A	A	25	A	55	55	—	A	56	51	90	107	A	192	A	137	A
P4		187	A	A	187	A	59	A	A	109	—	A	112	51	154	112	A	A	A	A	A

'A' indicates the *H. echinata* colony was alive at the end of the experiment. L = stolonless, I = intermediate, S = stoloniferous.

Fadden *et al.*, 1984), and consequently, *H. echinata* survival time was tested with respect to each measure separately. There is no significant correlation between the area covered by *H. echinata* stolons at the onset of interspecific contact and the length of time the colony withstood overgrowth by *P. carnea* (Kendall tau, $r = .12$, $P > .15$, $n = 42$), although survival time appears to be generally longer for colonies with large stolon networks (Fig. 3).

There is, however, a significant correlation between the length of time a genotype of *H. echinata* withstood overgrowth and the mat area of the colony at the onset of the interaction (Kendall tau, $r = .74$, $P < .001$, $n = 42$) (Fig. 4). There appears to be a survival threshold at a mat area of approximately 100 mm^2 . The frequency with which *H. echinata* colonies were overgrown by *P. carnea* is significantly higher among colonies with an initial mat area less than 100 mm^2 than among those in two larger size classes, $100\text{--}200 \text{ mm}^2$ and $>200 \text{ mm}^2$ ($\chi^2 = 17.8$, $df = 2$, $P < .005$) (Table IV). The survival rate of colonies does not differ between the two upper size classes ($\chi^2 = 0.03$, $df = 1$, $P > .80$). *H. echinata* colonies with small initial mat areas were usually killed after *P. carnea* had completely surrounded them and built up enough hyperplastic stolons around their periphery to extend completely across the mat. *H. echinata* colonies with large initial mat areas could not be surrounded by *P. carnea* due to their size and to the confines of the culture slides, and hence could not be overgrown.

DISCUSSION

The position occupied by a *H. echinata* colony on a limited substratum may significantly affect the outcome of competition between a colony of this species and

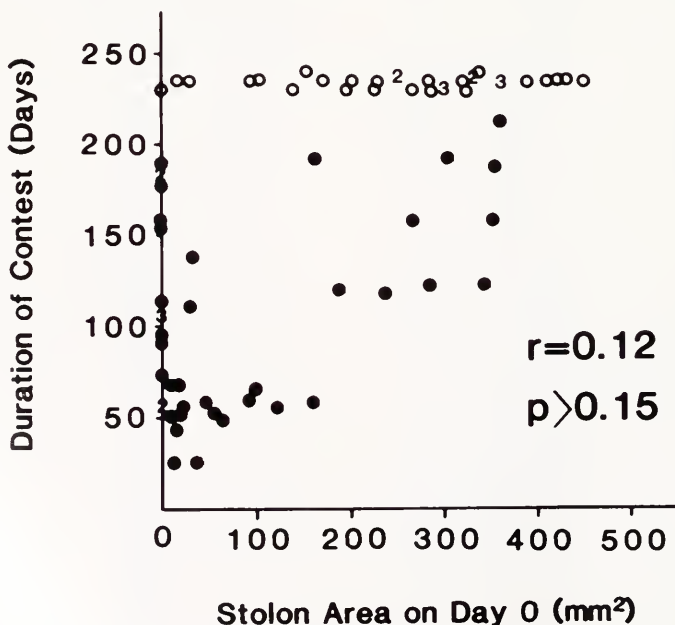


FIGURE 3. Correlation of the area covered by *H. echinata* stolons at the onset of an asymmetrical interspecific contest and the length of time the colony survived before being overgrown by *P. carnea*. Open circles represent colonies which remained alive at the end of the experiment. Numbers indicate multiple observations.

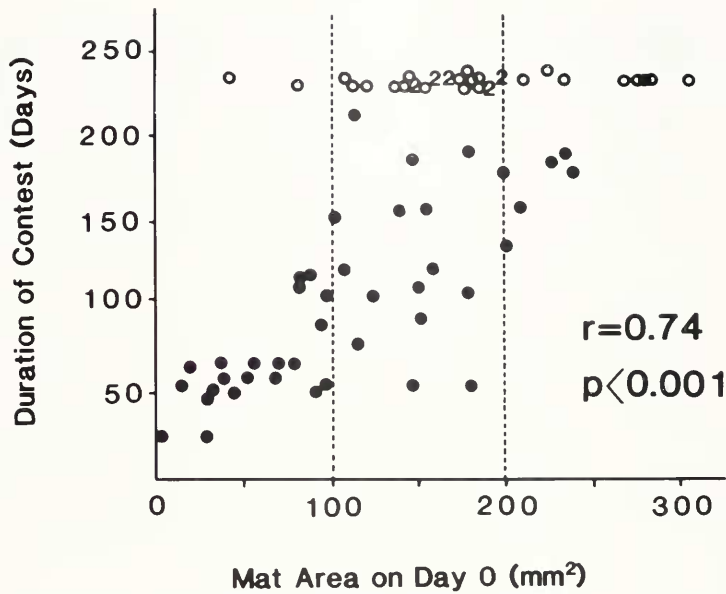


FIGURE 4. Correlation of the area of *H. echinata* mat tissue at the onset of an asymmetrical interspecific contest and the length of time the colony survived before being overgrown by *P. carnea*. Open circles represent colonies which were still alive at the end of the experiment. Numbers indicate multiple observations. Dashed lines demarcate the three size classes compared in Table IV.

one of *P. carnea*. The results presented above suggest that the ability of *P. carnea* to overgrow large *H. echinata* may depend on *P. carnea* first surrounding its competitor. Whether this condition can be met will be a function not only of the size of the *H. echinata* colony at the onset of the interaction, but also of the size of the free substratum, the position of the *H. echinata* colony relative to substrate boundaries, and the differential growth rates of the two species. Colonies with mat areas greater than 100 mm² at the time *P. carnea* was introduced reached the edges of the culture slides before *P. carnea* was able to surround them with its stolon network, and hence survived. Colonies initially smaller than 100 mm² were not growing rapidly enough to reach the limits of the slide before being surrounded by *P. carnea*.

The mat area threshold of 100 mm² above which *P. carnea* overgrows *H. echinata* is significant only in the context of the particular substrate employed in this study. In a substrate patch wider than 26 mm (the width of a Plexiglas slide), *P. carnea* should be able to surround and overgrow *H. echinata* colonies which are larger than 100 mm² at the onset of interspecific contact. A smaller substrate area, or the proximity of a

TABLE IV

Initial mat area (mm ²)	Number of <i>H. echinata</i> colonies overgrown by <i>P. carnea</i>	Number of <i>H. echinata</i> colonies surviving interaction
<100	21	2
100-200	16	23
>200	5	8

colony to a substrate boundary, will lower the size at which *H. echinata* colonies become safe from overgrowth. A colony which cannot be surrounded due to its proximity to a physical boundary will become safe from overgrowth at a size at which it could be overgrown were it instead surrounded by *P. carnea*. There will be a lower size limit to such a positional refuge: a very small *H. echinata* colony is likely to be overgrown by *P. carnea* regardless of its position on the substratum.

The interaction of colony size with position on the substratum may provide a refuge from competition on natural substrata. Many of the hermit crab shells on which *H. echinata* and *P. carnea* settle offer considerably less surface area than the slides used in this laboratory study. In addition, both the shell aperture and apex may operate as effective substrate barriers; a colony positioned along the aperture or around the apex of a shell will be difficult for another colony to surround. *H. echinata* planulae do recruit preferentially to points around the aperture of a shell (Teitelbaum, 1966). If new recruits of both species recruit simultaneously and in similar locations on the same shell it is likely that *P. carnea* will overgrow *H. echinata* and monopolize the substratum. If *P. carnea* recruits to a shell with an already established *H. echinata* colony, the result will be either overgrowth of the *H. echinata* colony and monopolization of the entire shell by *P. carnea*, or, alternatively, a "standoff" between the two species with maintenance of a static boundary between them (see Connell, 1976; Karlson, 1980).

The results of interspecific encounters in the laboratory suggest that, were all else equal, *P. carnea* should eventually competitively exclude *H. echinata* on hermit crab shells. However, data on the distribution and frequency of occurrence of these two species in Long Island Sound do not support this prediction. In all seasons, *H. echinata* is much more abundant than *P. carnea*: from June through October, 1982, only approximately 7% of all hydroid-encrusted shells collected were occupied by *P. carnea*, while *Hydractinia* colonies occupied the remaining 93% (Buss, Yund, and Harrison, in prep.). Competition, evidenced by hyperplastic stolons, occurs frequently between colonies of *H. echinata* which occupy the same shell. However, contact between *H. echinata* and *P. carnea* was observed only once from over 1000 hydroid-occupied shells collected (Buss, Yund, and Harrison, in prep.). This low rate of encounter between *P. carnea* and *H. echinata* is a product of the low frequency of occurrence of *P. carnea* combined with the probability that individuals of both species will colonize the same shell. Early competitive exclusion of *H. echinata* by *P. carnea* when both recruit to the same shell may also contribute to the low observed encounter rate.

Models of a two-species community in which one species is the dominant competitor predict that a population of the inferior species can be maintained if there is a concomitant difference in the recruitment ability of the two species such that the inferior competitor is able to recruit to unoccupied substrata more quickly or more reliably than the dominant competitor (Armstrong, 1976). In a system in which a size refuge from competition is in operation, a difference in rate of recruitment, or in the seasonal timing of recruitment, may enable the inferior competitor to grow to a safe size before the dominant competitor can recruit onto the open substratum (Sebens, 1982). Higher rates of post-recruitment mortality of the superior competitor, or frequent interference with its overgrowth ability by events such as partial predation, are additional mechanisms which would allow an inferior competitor to reach a size refuge before being overgrown.

There is some evidence that the failure of *P. carnea* to displace *H. echinata* on hermit crab shells, despite its competitive superiority, may be due to a low rate of recruitment of this species to hermit crab-inhabited shells. In Long Island Sound, recruits of *P. carnea* (small colonies occupying less than 30% of the shell surface) were

found on only 0.2% of all shells collected from June to October, 1982, ($n = 1663$), whereas *H. echinata* recruits were present on 22% of these shells (Buss, Yund, and Harrison, in prep.). Because recruitment of *P. carnea* is apparently a rare event in this community, most *H. echinata* colonies will reach a size at which they are safe from overgrowth without ever encountering *P. carnea*. Yet the competitive superiority of *P. carnea* in interspecific contests ensures that an individual which does successfully recruit to a hermit crab shell can acquire and maintain space on that shell even if it is already occupied, or subsequently invaded, by *H. echinata*.

The asymmetry in the degree of interspecific recognition displayed by these two species can be interpreted in light of the rate at which they are likely to encounter one another in the field. *H. echinata* is one of the most abundant members of the hermit crab epifaunal community (Karlson and Shenk, 1983), and there is a high rate of encounter of this species with conspecifics and with other common epifaunal species, such as the bryozoan, *Alcyonidium polyomm* (Karlson and Shenk, 1983). However, the probability that an individual of *H. echinata* will encounter *P. carnea* during its lifetime is relatively low; consequently, there should be little selective pressure acting to maintain its ability to recognize this uncommon species as a potential competitor. As shown, *H. echinata* does not produce hyperplastic stolons in response to contact with *P. carnea*. *P. carnea*, on the other hand, has a high probability of encountering a *H. echinata* colony upon recruiting to a hermit crab shell, due to the high percentage of all shells which are occupied by this species. Selection should act on *P. carnea* to maintain a mechanism for recognition and subsequent deployment of competitive structures against this important interspecific competitor.

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